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OXYGEN CONSUMPTION AND RESPIRATORY ENERGETICS IN THE SPINY LOBSTER, *PANULIRUS INTERRUPTUS* (RANDALL)

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This paper is part of a series designed to examine trophic and energy relationships in large decapod crustaceans. Information about metabolic rates, generally determined by measuring oxygen consumption (QO_2), and metabolic regulatory mechanisms is of basic importance in defining the metabolic energy budget (Paine, 1965) of an animal. Metabolic rates determine the amount of energy expended in producing biomass and therefore are also of importance in determining the role of the animal in community metabolism. Little information of this nature has been published on palinurids, and none on the California spiny lobster, *Panulirus interrupts,* an exemplary decapod.

In general, animals are either oxygen regulators or conformers according to the dependency of their rate of oxygen consumption on oxygen concentration (pO_2) in the environment. Regulating animals maintain a fairly constant rate of metabolism throughout a range of O_2 concentration. At some critical pO_2 (P_c) less than saturation, these animals will cease to regulate and will become dependent on the external pO_2. Most aquatic vertebrates, all known terrestrial vertebrates, and probably all terrestrial insects are regulators (Prosser and Brown, 1961). Conformers are animals whose metabolism is entirely dependent on the environmental pO_2. Fewer animal groups exhibit this mechanism. Most parasitic worms plus some crustaceans are conformers (Wolvekamp and Waterman, 1960; Prosser and Brown, 1961).

The dependency of QO_2 on body weight is a well-documented phenomenon in the animal kingdom and seems to be most evident in animals weighing between 1 and 1000 g (Edwards, 1946; Zeuthen, 1953; Wolvekamp and Waterman, 1960; Prosser and Brown, 1961). Most specimens of postpuerulus *P. interruptus* sighted or sampled by the author near San Diego, California are included within this weight range. It is also well-documented that, in poikilotherms, metabolism generally varies directly with the environmental temperature (Prosser and Brown, 1961).

In this study weight-specific respiration rates and the effects of environmental oxygen concentration, body weight, environmental temperature, and level of animal activity on these rates were determined for *P. interruptus* as a measure of metabolic energy lost under various conditions. The rates of energy expended in the process of active and resting metabolism, expressed as cal/g/day, were derived from these data by appropriate conversions.

Materials and Methods

Specimens of *P. interruptus* (an eastern North Pacific palinurid of commercial importance)used in this study measured 4–9 cm from the eyes to the posterior end

of the cephalothorax (carapace length). This size range included the majority of lobsters found near San Diego, California, where the sample population was obtained during the spring of 1967. Animals to be used in respiration measurements were held in 75-liter aquariums at 16° C and fed on the flesh of the California mussel, *Mytilus californianus*. Only those lobsters that fed in the laboratory were used.

Respiration rates of individual *P. interruptus* were measured by using a 24.0 × 9.4 × 15.1 cm (15 liter) rectangular plexiglass chamber fitted with a respiration head which was sealed by two rubber "O" rings in an 18.3 cm diameter opening in the top of the chamber. The head had an opening for insertion of a Yellow Springs BOD type polarographic oxygen electrode (Kanwisher, 1959) and two plexiglass pipes which were connected to a pump for circulating water through the respiration chamber. The exhaust pipe was directed downward for maximum circulation of water within the chamber; the intake pipe was directed horizontally and ended just under and to the side of the electrode membrane, in order to draw water across it. The chamber had a small hole fitted with a rubber stopper for insertion of a thermometer and for removal of water when the respirometer was not in operation.

In order to facilitate the removal of trapped air from the system, the respirometer was submerged in a plexiglass aquarium filled with sea water. The aquarium and water circulating tubing were placed in a 190 liter (50 gal) water bath. Another larger hose from the exhaust of the water bath pump was coiled around the respirometer inside the aquarium in order to increase cooling efficiency. All respiration determinations were made with the cover of the water bath closed. The entire system allowed the temperature of the sea water inside the respirometer to to be maintained within ±0.3° C. This procedure also maintained the animal in darkness and free from external laboratory disturbances during the measurements.

The oxygen electrode was connected through a Yellow Springs Instrument bridge circuit to a variable span stripchart potentiometer recorder, which allowed continuous monitoring of oxygen concentration in the respirometer. The polarographic electrode system was calibrated for air saturation level of oxygen concentration by placing an air stone and the electrode in a beaker of sea water at the experimental temperature for 5–10 min and adjusting the bridge circuit.

The respirometer system was filled with natural sea water filtered through coarse, crepe-surface filter paper and adjusted to the experimental temperature. Preceding each respiration determination, a control run of approximately one hour was made without the lobster in the chamber to determine the effect of bacterial respiration and possible unknown effects on the potentiometer recordings. This was followed by a 2–3 hour run with the lobster in the chamber. After each run the wet weight of the animal was recorded after vigorously shaking the animal to remove excess water. The temperature of the water in the respirometer was determined at the beginning and end of the control and experimental runs. The water in the respirometer was changed before each run and in the aquarium containing the respirometer every third run, for occasionally there was some exchange of water due to handling between the respiration chamber and the aquarium before and after each run.

Experimental animals were placed without food in a second plexiglass aquarium in the water bath to allow them to acclimate to the experimental conditions and temperature for 24 hours prior to placing them in the respirometer. Twenty-four hours was considered sufficient time for the animals to adjust to the small differences

between the temperature of the holding tanks and the experimental temperatures. Respiration measurements were made on 10 lobsters at 13° C, 12 lobsters at 16° C, and nine lobsters at 20° C. These temperatures encompass the normal temperature range to which this species is subjected in nature.

In order to examine the effect of pO_2 on weight-specific oxygen consumption (QO_2), respiration rates were determined separately within the following pO_2 ranges for all respiration records:

pO_2 Range	Mean pO_2
6.5–6.0	6.25
6.0–5.5	5.75
5.5–5.0	5.25
5.0–4.5	4.75
4.5–4.0	4.25
4.0–3.5	3.75
3.5–3.0	3.25
3.0–2.5	2.75
2.5–2.0	2.25
2.0–1.5	1.75
1.5–1.0	1.25
1.0–0.5	0.75

The change in oxygen concentration (ppm/hr) was determined by dividing each 0.5 ppm increment by the time period between the limits of the increment of a given pO_2 range. The respiration chamber, hoses, and pump contained a total water volume of 15.42 liters. The change in oxygen concentration/hr was converted to oxygen consumption in ml/hr, based on the volume of the respirometer minus the volume of the lobster and the relationship: 1 ppm = 0.698 ml O_2/1 water. The volumes of representative lobsters were measured by water displacement and are given below:

Carapace length (cm)	Vol (liter)
5	0.08
6	0.16
7	0.21
8	0.43
9	0.63

The resultant oxygen consumption value was divided by the weight of the animal to obtain the weight-specific oxygen consumption in ml/g/hr for each pO_2 range.

In order to examine the effect of pO_2 on QO_2, standard linear and curvilinear regression analyses (Steel and Torrie, 1960) were made on these variables. Analyses of variance (Steel and Torrie, 1960) were used to test for the significance of the linear and curvilinear regressions. Analyses of variance were also used to test for the significance of curvilinearity, that is, whether the use of the 2nd degree polynomial reduced the variance about the regression line significantly more than did the linear regression.

The QO_2 is, of course, highly influenced by activity. Resting metabolism is distinguished from basal metabolism, which is difficult to determine in any animal except man. The QO_2 of *P. interruptus,* measured while the animal remained motionless and relaxed for a period of an hour or more, was assumed to represent resting metabolism. The lobsters were generally excited and moved about actively when

placed in the respirometer. Inspection of the slopes of the respiration records suggests that the animals required approximately 30 minutes to settle down to a uniform low level of metabolic activity. It was assumed that the level of activity exhibited by individuals during the initial 30 minute period was representative of their peak level of activity in nature while foraging for food. The remainder of the run was used to determine resting metabolism.

P. interruptus remains fairly passive during the daylight hours, but begins foraging for food at sundown and continues until sunrise (Winget, unpublished). Therefore, the daily oxygen consumption is a combination of resting and active rates. One method of determining the mean daily rate would be to assume that half of the 24-hour period is spent in a state of active metabolism and half in a state of resting metabolism. This assumes, however, that the animal is continually active throughout the 12-hour period of darkness and is probably an overestimation.

An adaptation of a model proposed by McNab (1963) for the energy budget of a mouse gives a more accurate and conservative estimate of the daily oxygen consumption. This estimate is expressed in the equation:

$$M = f(T_c) + g(t)$$

where

M = metabolism
$f(T_c)$ = the passive rate as a function of time at a constant temperature,
$g(t) = \frac{1}{2}M_a[\cos(kt) + |\cos(kt)|]$ and expresses the increment of O_2 consumption due to activity as a function of time,
M_a = the increment at peak activity, and

$\cos(kt) + |\cos(kt)|$ = an expression of periodicity.

This model divides a period, such as 24 hours, into two parts: one where $g(t) = 0$, and one where $g(t)$ is greater than 0. The constant k aligns the x axis along the desired time scale. For this paper, $k = \pi/12$. At t_0 (midnight), $\cos(kt) = 1$ and $g(t) = M_a$. From t_6 to t_{18} $\cos(kt)$ is negative and $g(t) = 0$. At t_{24}, $g(t) = M_a$ again. To determine the total oxygen consumption over a 24-hour period, M is used as a derivative with respect to t and integrated from $t = 0$ to $t = 24$.

Results and Discussion

Effect of environmental oxygen concentration

Weight-specific oxygen consumption during resting metabolism and the effect of pO_2 on $\dot{Q}O_2$ at 13°, 16°, and 20° C for 31 specimens of *P. interruptus* are given in Table I. The mean of each pO_2 range was used as the independent variable in the regression analyses described in the Materials and Methods section. These variables were divided into groups and considered separately for each temperature as follows:

13° C pO_2(ppm)	16° C pO_2(ppm)	20° C pO_2(ppm)
6.50–4.75	5.25–2.75	4.75–2.75
4.25–3.25	2.25–0.75	2.25–0.75
6.50–3.25		
2.25–1.25		

In order to reduce the influence of differences in body weight on the regressions, the QO_2's corresponding to lobster weights of 0–199, 200–299, 300–399, 400–499, and 500–599 g were analyzed as separate sets of dependent variables. The variables used in each individual analysis are separated by lines in Table I. Only those groups of data which contain four or more QO_2 values were used.

TABLE I

Weight-specific oxygen consumption in ml/g/hr during resting metabolism of P. interruptus

Wet body weight (g)	ET* °C	QO_2 during resting metabolism at pO_2 levels between 0.5–6.5 ppm											
		$\bar{X}$ 6.5–6.0 6.25	6.0–5.5 5.75	5.5–5.0 5.25	5.0–4.5 4.75	4.5–4.0 4.25	4.0–3.5 3.75	3.5–3.0 3.25	3.0–2.5 2.75	2.5–2.0 2.25	2.0–1.5 1.75	1.5–1.0 1.25	1.0–0.5 0.75
56.0	13	0.0766											
100.8			0.0638	0.0532									
214.0			0.0498	0.0498	0.0498								
233.8		0.0330	0.0281	0.0281									
243.5						0.0437	0.0375	0.0375					
279.4				0.0207	0.0207								
293.9					0.0310	0.0361	0.0361	0.0361					
328.4			0.0388	0.0277	0.0242	0.0277							
342.7						0.0420	0.0265	0.0265	0.0327	0.0265			
393.6					0.0367	0.0367	0.0367	0.0367	0.0287	0.0234	0.0196	0.0128	
216.4	16					0.0509	0.0360						
245.0						0.0589	0.0589	0.0498	0.0498	0.0366	0.0281		
250.0							0.0539	0.0326	0.0265	0.0219	0.0219	0.0132	
202.0								0.0470	0.0572	0.0290	0.0290	0.0170	
335.4					0.0476	0.0633	0.0633	0.0476	0.0476	0.0476	0.0317		
354.5						0.0476	0.0476	0.0476	0.0327	0.0327	0.0236	0.0133	0.0077
364.5								0.0627	0.0509	0.0364	0.0364	0.0176	0.0120
366.6								0.0578	0.0462	0.0462	0.0230	0.0172	0.0076
420.7				0.0497	0.0497	0.0373	0.0497	0.0373	0.0373	0.0373	0.0373		
429.9					0.0582	0.0488	0.0417	0.0488	0.0488	0.0292	0.0243		
524.3								0.0589	0.0394	0.0394	0.0296	0.0236	
578.7								0.0429	0.0429	0.0357	0.0268	0.0214	0.0089
124.3	20				0.0938	0.0938	0.0766	0.0644					
155.5						0.1290	0.0738	0.0738	0.0738	0.0502			
171.0							0.0658	0.0658	0.0658	0.0533	0.0378		
204.7									0.0629	0.0520	0.0258	0.0184	
227.1							0.0533	0.0845	0.0612	0.0612	0.0470	0.0377	
255.9								0.0758	0.0758	0.0758	0.0425	0.0425	0.0177
372.6							0.0841	0.0561	0.0561	0.0561	0.0422	0.0210	
379.4									0.0579	0.0579	0.0388	0.0330	0.0192
387.9							0.0648	0.0648	0.0648	0.0462	0.0270	0.0231	

* Environmental temperature.

In those ranges where the mean pO_2 was 2.25 ppm or less, four out of seven curvilinear and five out of seven linear regressions were significant ($p < 0.05$). In no case was curvilinearity significant ($p > 0.05$). In those ranges where the mean pO_2 was 2.75 ppm or greater, one out of 13 linear regressions was significant ($p < 0.05$). The single significant regression was for variables corresponding to lobsters at 20° C which weighted less than 200 g.

Regulation of oxygen consumption

The results of the analyses indicate that, in general, the QO_2 of *P. interruptus* is not affected by oxygen concentration at pO_2 levels above 2.5 ppm, but that QO_2 declines at pO_2 values less than 2.5 ppm. The conclusion of this study is that *P. interruptus* is a regulator and that P_c is approximately 2.5 ppm. More extensive

analyses, incorporating larger sample sizes and regression analyses of data above and below pO_2 values close to 2.5 ppm are needed to depict more accurately the range of pO_2 values within which P_c falls. However, examination of the increasing or decreasing trends of the individual QO_2 values in Table I suggests that P_c lies between 2 and 3 ppm, or 25–40% air saturation. The P_c for *P. interruptus* is similar to those of two crayfish, *Orconectes* (20–40% air saturation) and *Astacus* (20% air saturation), and other regulatory crustaceans reported by Weymouth, Crismon, Hall, Belding, and Field (1944); Wolvekamp and Waterman (1960); and Prosser and Brown (1961).

If the QO_2–pO_2 relationships of *P. interruptus* are representative of *Panulirus* and related genera, this aspect of metabolism represents a distinctive physiological contrast between spiny lobsters (family Palinuridae) and lobsters of the family Homaridae. Thomas (1954) indicated that the QO_2 of *Homarus vulgaris* varies directly with the oxygen concentration of the water. It has also been shown that *H. americanus* (Amberson, Mayerson, and Scott, 1924) and *H. gammarus* (Wolvekamp and Waterman, 1960) are conformers, as are the crayfish, *Cambarus* (Maloeuf, 1936), the crab *Callinectes* (Wolvekamp and Waterman, 1960) and the horseshoe crab, *Limulus* (Prosser and Brown, 1961).

The mechanisms through which the regulation of oxygen utilization in crustaceans is effected are mainly circulatory and ventilation adaptations to changes in various environmental parameters (Prosser and Brown, 1961). Redmond (1955) found that the blood of *P. interruptus* reaches 95% saturation when the partial pressure of oxygen is about 15 mm Hg (9.4% air saturation) at 10° C, 25 mm at 15° C, and 30 mm at 20° C. The half saturation points (P_{50}), a more accurately determined figure for oxygen affinity, are 4, 6.5, and 9 mm, respectively. Redmond has determined, however, that even in highly oxygenated water, the immediate post branchial blood in *P. interruptus* is only about 50% saturated. This phenomenon indicates that oxygen diffusion across the gill surfaces is very slow and that the pO_2 may drop from near saturation to less than 10 mm Hg (6.3% air saturation). The finely branched gills are distributed over the entire lateral surface of the carapace and present a tremendous surface for exchange of O_2 and CO_2 with the ventilated water. This large gill area undoubtedly compensates for the low diffusion gradient. The lack of blood saturation, even under highly oxygenated environmental conditions, would indicate that QO_2 regulation is probably not affected appreciably by differential uptake of O_2 by the blood. To my knowledge, it is not known whether changes in pO_2 alter the heartbeat.

No specific information is available on the ventilation rates of *P. interruptus*. However, it is suspected that regulation of QO_2 may be through ventilation control. The ventilation rate of the oxygen conformer, *Homarus*, does not change under low pO_2's (Thomas, 1954). Fox and Johnson (1934) found that the crayfish, *Astacus fluviatilis*, regulates at least partially through ventilation control. When the pO_2 was lowered from 8.3 to 2.2 ml O_2/l, the scaphognathite beat increased from 34 to 140 beats/min in this species.

The relationship between QO_2 and environmental oxygen supply has been discussed extensively in the literature. For many marine animals, including *P. interrupts*, this is probably a purely academic consideration, for they rarely exist under conditions of low oxygen supply. Serial dissolved oxygen measurements obtained

at the U. S. Naval Electronics Laboratory Tower off Mission Beach, California (Ramsey, 1962) indicate that pO_2's from the surface to the bottom at a depth of 20 meters deviate little from air saturation levels. *P. interruptus* is usually found in similar areas of shallow, well-circulated water where the pO_2 is very close to saturation at all times. The analyses of the QO_2–pO_2 relationships of *P. interruptus* was undertaken to compare the dependency of the QO_2 of this species on oxygen concentration with this relationship of other crustaceans and to attempt to apply a method of determining meaningful QO_2 values which were measured over a wide range of oxygen concentrations, a problem which represents one of the major shortcomings of the type of respirometer system used in this study.

Weight-specific respiration rates

Because the regression analyses indicate that, in general, the QO_2 does not change significantly when measured from a mean pO_2 of 2.75 ppm (range 2.5–3.0

TABLE II

Weight-specific oxygen uptake in P. interruptus *during resting metabolism in ml/g/hr*

Wet body weight (g)	Mean QO_2 from 6.5–2.5 ppm	Mean temperature of experiment (°C)	Wet body weight (g)	Mean QO_2 from 5.5–2.5 ppm	Mean temperature of experiment (°C)	Wet body weight (g)	Mean QO_2 from 5.0–2.5 ppm	Mean temperature of experiment (°C)
56.0	0.0766	12.8	216.4	0.0435	16.0	124.3	0.0822	19.8
100.8	0.0585	12.9	245.0	0.0544	15.9	155.5	0.0876	19.9
214.0	0.0498	12.5	250.0	0.0377	15.9	171.0	0.0658	19.9
233.8	0.0297	13.3	302.0	0.0521	16.0	204.7	0.0629	19.8
243.5	0.0396	12.5	335.4	0.0539	16.1	227.1	0.0663	19.8
279.4	0.0207	12.9	354.5	0.0439	15.9	255.9	0.0758	19.8
293.9	0.0348	13.0	364.5	0.0568	15.9	372.6	0.0654	19.6
328.4	0.0296	12.6	366.6	0.0521	15.5	379.4	0.0578	19.7
342.7	0.0319	13.0	420.7	0.0435	16.0	387.9	0.0648	19.8
393.6	0.0351	12.6	429.9	0.0492	16.0			
			524.3	0.0492	16.0			
			578.7	0.0429	15.9			

ppm) up to the highest pO_2 used in the experiments, the QO_2 for each lobster was determined as an average of those values measured at pO_2's higher than 2.5 ppm. These QO_2's are given in Table II.

In order to examine the effect of body weight on QO_2, standard linear and curvilinear regression analyses (Steel and Torrie, 1960) were made on these variables. The significance of the regressions was tested with analysis of variance (Steel and Torrie, 1960). These regression analyses of the QO_2's in Table II on body weight and tests of significance were repeated with the data for individuals weighing less than 200 g deleted, in order to examine the influence of these smaller individuals on the regressions.

The results indicate that the QO_2 for *P. interruptus* weighing from 200–600 g is not significantly ($p > 0.05$) affected by body weight. At 13° C significant ($p < 0.05$) linear and curvilinear regressions appear when data for individuals weighing less than 200 g are included (curvilinearity significant, $p < 0.05$). QO_2's for

individuals weighing less than 200 g were not measured at 16° C. More data are needed to determine the effect of body weight on QO_2 for individuals weighing less than 200 g. However, it is suspected, based on the available data, that the effect is significant.

Thomas (1954) presented a graph of the regression of QO_2 on body weight in *Homarus vulgaris*. The standard linear regression and analysis of variance test of the significance of the regression (Steel and Torrie, 1960) were run by the author on values for weight and QO_2 estimated from Thomas's graph. The regression was

TABLE III

Oxygen consumption in ml/g/hr in decapod crustaceans

Species	Wet body weight (g)	Temperature (°C)	QO_2 (ml/g/hr)	Reference
Macrura				
Scyllaridae				
Palinurus elephas	—	15	0.044	Wolvekamp and Waterman (1960)
Panulirus interruptus	200–600	13	0.034	This study
		15	0.048	
		16	0.048	
		20	0.066	
P. argus	300	30	0.091**	Maynard (1960)
Nephropsidae				
Homarus americanus	189	15	0.035	Thomas (1954)
	230	22	0.037	
	324	22	0.039	
H. vulgaris	400*	15	0.063*	Thomas (1954)
	680*	15	0.040*	
H. gammarus	—	15	0.068	Wolvekamp and Waterman (1960)
Orconectes immunis	—	25	0.160–0.170	Wolvekamp and Waterman (1960)
Brachyura				
Carcinus maenas	—	16	0.052–0.071	Wolvekamp and Waterman (1960)
Cancer pagurus	—	16	0.107	
Ocypode quadrata	—	26	0.196	
Pugettia producta	—	15	0.032–0.170	
Mean of 54 crustaceans	—	15	0.108	Wolvekamp and Waterman (1960)

* Values approximated from graphs (Thomas, 1954).
** Calculated from formula $QO_2 = 0.24W^{-0.17}$ (Maynard, 1960).

significant ($p < 0.05$) and indicates that in *H. vulgaris*, QO_2 is dependent on body weight. This dependency may illustrate another physiological contrast between the Palinuridae and Homaridae. If *P. interruptus* is representative of Palinuridae metabolism, the QO_2 of this group of animals may be independent of body weight within the 200–600 g range.

In the absence of significant regression ($p > 0.05$) for animals larger than 200 g, mean QO_2's corresponding to these animals were used to predict the oxygen consumption of *P. interruptus*. At 13°, 16°, and 20° C, the QO_2 is 0.0339, 0.0483,

and 0.0655 ml/g/hr, respectively. These values are compared with QO_2's of other decapod crustaceans in Table III. At 15° and 16° C, the QO_2 of *P. interruptus* is similar to that of another palinurid, *Palinuris elephas*. From the data in Table III, QO_2's for the palinurids appear to fall within the range of values for homarids, but are generally a little lower than the astacid, *Orconectes,* and the Brachyura.

The relationship between oxygen consumption and body weight is often expressed by the equation:

$$\log O_2 = \log a + b \log W$$

or

$$O_2 = aW^b,$$

when

a = the y intercept,
b = the regression slope, and
W = the weight.

When determining values for this equation, oxygen is measured as total O_2 consumption of the animal/hr and not on a weight-specific basis.

Whole animal oxygen consumption values for *P. interruptus* were determined by multiplying the QO_2's in Table II by the corresponding body weights of the experimental animals. Analyses were made of the regressions of these nonweight-specific O_2 consumption values on animal body weight in logarithmic form. The y intercept and slope of the regression line at each temperature are presented below:

a		b	
Log	Non-log		Temperature (°C)
−0.2120	0.614	0.483	13
−1.1447	0.072	0.935	16
−0.5972	0.253	0.763	20

Although the b values vary considerably, their average is 0.73.

Zeuthen (1953) made a similar analysis of large poikilotherms, including crustaceans, amphibians, fish, and reptiles, and obtained an average slope of 0.76, a very similar value to the slope obtained in this study for *P. interruptus*. Zeuthen (1953) states that the QO_2 of homeotherms varies with a power of about 0.75 (b value) of the body weight. Weymouth *et al.* (1944) reported that the QO_2 of the kelp crab, *Pugettia producta,* is inversely proportional to the size of the animal (b = 0.788). They also plotted the log O_2 and log weight of various Crustacea from 27 mg to 520 g with a resultant composite slope of 0.826. Paine (1965) obtained a b value of 0.885 for the opishthobranch, *Navanax inermis,* and Richman (1958) obtained a slope of 0.881 for *Daphnia pulex*. Thus it appears that the slope of oxygen consumption plotted against weight on double logarithmic paper for *P. interruptus* is close to poikilotherms in general but a little lower than many other crustaceans.

Effect of environmental temperature

Standard regression analysis and analysis of variance test of significance (Steel and Torrie, 1960) of the QO_2's on mean temperatures for all body weights in Table II show a significant linear regression ($p < 0.05$). The linear equation is:

$$Y = 0.00418X - 0.0150$$

Predictions of QO_2's at temperatures other than those measured may also be obtained with the Q_{10}, the factor by which chemical and physical reactions are accelerated due to a 10° C change in temperature, obtained from the formula:

$$Q_{10} = \left(\frac{K_1}{K_2}\right)^{10/(t_1-t_2)}$$

where in metabolic studies,

K_1 = the QO_2 at t_1 (temperature, °C), and
K_2 = the QO_2 at t_2.

Using QO_2 values of 0.0339, 0.0483, and 0.0655 for temperatures of 13°, 16°, and 20° C, respectively, the Q_{10} for *P. interruptus* in the temperature range of 13–16° C is 3.25, and for 16–20° C it is 2.14. These values are similar to Q_{10}'s for crustaceans and poikilotherms in general (Wolvekamp and Waterman, 1960; Prosser and Brown, 1961).

TABLE IV

Weight-specific oxygen uptake in P. interruptus *during active metabolism in ml/g/hr*

Wet body weight (g)	QO_2 at 13°C (ml/g/hr)	Wet body weight (g)	QO_2 at 16°C (ml/g/hr)	Wet body weight (g)	QO_2 at 20°C (ml/g/hr)
56.0	—	216.4	0.1001	124.3	0.1197
100.8	—	245.0	0.1044	155.3	—
214.0	0.0747	250.0	0.0750	171.0	0.0845
233.8	0.0618	302.0	0.0832	204.7	0.0778
243.5	0.0656	335.4	0.0792	227.1	0.0956
279.4	—	354.5	0.0776	255.9	0.0965
293.9	0.0723	364.5	0.0870	372.6	0.1196
328.4	0.0485	366.6	0.0827	379.4	0.0947
342.7	0.0649	420.7	0.0622	387.9	0.1058
393.6	0.0585	429.9	—		
		524.3	0.0886		
		578.7	0.0670		

Effect of animal activity

The QO_2 values determined during active metabolism, as described in the Materials and Methods section, are given in Table IV. Activity will obscure any relationship between QO_2 and weight or pO_2. The mean of the active QO_2 values at each temperature was therefore used as the best estimate. These are: 0.0638, 0.0825, and 0.0983 ml/g/hr at 13°, 16° and 20° C, respectively. These values along with the QO_2's for resting metabolism were used in the McNab model described in the Materials and Methods section to determine oxygen consumption over a 24-hour period.

At 13° C, the integral from this model is:

$$\int_0^{24}\left[.0339 + \frac{.0299}{2}\left(\cos\frac{\pi}{12}t + \left|\cos\frac{\pi}{12}t\right|\right)\right]dt$$

Using similar integrals for the other temperatures, daily oxygen consumptions were estimated to be 1.04, 1.42, and 1.82 ml/g at 13°, 16°, and 20° C, respectively. The active increment is similar for all three temperatures (0.229, 0.261, and 0.251 ml/g), indicating that it is not influenced appreciably by temperature.

Metabolic rates in caloric form

Vonk (1960) concludes from data reported by Renaud (1949) for the crab, *Cancer pagurus,* that the chief energy source in this species is the metabolism of glycogen and fatty acids and indicates that this is probably true for crustaceans in general. No data are available on the composition of *P. interruptus.* However, the composition of many decapod crustaceans is probably fairly similar. Therefore, data on the composition of *C. pagurus* were used. Vonk gives the per cent of fresh weight of glycogen and fatty acids in *C. pagurus* as 0.20 and 1.67, respectively. These are average values, for the composition of decapods varies with the molting cycle.

Brody (1964) lists the energy values liberated for fat and glycogen when burned with 1 ml of oxygen as 4.6 and 5.14 cal, respectively. The mean of these values, weighted by the per cent composition of each, or 4.66 cal/ml O_2 consumed, was used to determine the metabolic expenditure of energy in *P. interruptus.* This value is slightly less than 5.0 used by Paine (1965) for *Navanax inermis,* by Richman (1952) for *Daphnia pulex,* and 4.8 used by Golley and Gentry (1964) for the harvester ant, *Pogonomyrex badius.*

When the daily oxygen consumption is multiplied by 4.66, the mean energy utilized in metabolism by *P. interruptus* at 13°, 16°, and 20° C is 4.85, 6.62, and 8.48 cal/g/day, respectively, for individuals in the range of 200–600 g during the intermolt period.

Conclusions

The amount of energy expended by *P. interruptus* in converting ingested food to utilizable substances or in metabolizing reserve energy sources during the intermolt period is estimated to vary between 5 and 8 cal/g/day throughout the year. A comparison of QO_2 values for *P. interruptus* and other decapod crustaceans indicates that 5–8 cal/g/day is a rough estimate of daily metabolism in other palinurid and homarid lobsters and that a slightly higher value would apply in several crab species. However, knowledge of diurnal metabolism in these species is necessary to substantiate this conclusion. If it is assumed that the average weight of *P. interruptus* near San Diego, California is between 200 and 300 g, the daily metabolic energy loss is on the order of 1.0–1.5 kcal per individual during the winter and 1.5–2.5 kcal during the summer.

This paper only initiates a determination of the role of a large decapod in community metabolism. For a complete study, estimates are needed of metabolic energy lost during all stages of the molting cycle as well as knowledge of population structure and dynamics of the species involved.

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Summary

This paper is part of a series designed to examine the trophic and energy relationships of large decapod crustaceans. The oxygen consumption and daily energy loss due to respiration were measured in the California spiny lobster, *Panulirus interruptus*. At 13°, 16°, and 20° C, the QO_2 was 0.0339, 0.0483, and 0.0655 ml/g wet body weight/hr, respectively, for individuals weighing between 200 and 600 g. Within this weight range QO_2 was independent of body weight but was dependent on temperature, yielding a Q_{10} estimate of 3.25 from 13°–16° C and a corresponding coefficient of 2.14 from 16°–20° C. The QO_2 of this species is fairly similar to that of other palinurid and homarid lobsters and somewhat lower than those of several crab species. *P. interruptus* is an oxygen regulator, with P_c located between 25 and 45% air saturation.

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